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RELATIONS BETWEEN UNIT-GROUPS OF BONOBOS AT WAMBA, ZAIRE: ENCOUNTERS AND TEMPORARY FUSIONS

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ABSTRACT Inter-group relations among wild bonobos (*Pan paniscus*) at Wamba, Zaire, are described. Members of two habituated unit-groups were frequently observed to intermingle, mainly at artificial feeding sites, but also in natural vegetation. During such encounters various affinitive behaviors, such as genito-genital rubbing, copulation, and peering were observed between members of different groups. Affinitive interactions between females of different unit-groups were particularly prominent, and appeared to ease the tension caused by the encounter. Males interacted with members of the other group much less frequently than females. Aggressive interactions between members of different groups were rare. Young nulliparous females were observed to transfer between unit-groups during encounters. These observations suggest that bonobos have a regional society above the unit-group level, which is unique among nonhuman primates for which comparable data are available.

Key Words: Bonobo; *Pan paniscus*; Inter-group encounters; Social behavior; Human evolution.

INTRODUCTION

While most studies of primate social behavior have concerned relationships within social units, there is also a growing body of information on interactions between social units (Crook, 1966; Kummer, 1968; Kawai et al., 1983; Cheney, 1987; and References therein). In general, these studies have found that most interactions between groups are antagonistic or aggressive in nature. The present paper reports on inter-unit-group relations, including those which are truly friendly and affinitive, observed in bonobos (*Pan paniscus*), and discusses the significance of such relationships in the evolution of primate society.

The home ranges of bonobo unit-groups at Wamba overlap considerably with one another (Kano & Mulavwa, 1984). An earlier study found that when two unit-groups were observed to encounter one another, members of each group avoided those of the other, and few affinitive interactions were recorded between them. Thus relations between unit-groups were thought to be antagonistic (Kuroda, 1982). In a more recent study, however, two unit-groups were observed to spend hours peacefully together following an encounter, and in some cases they moved and foraged together (Idani, 1991). It cannot be concluded that the relationship between these unit-groups was simply antagonistic or hostile (Kano, 1986).

Relations between unit-groups have been little studied owing to the difficulty in directly observing encounters. For bonobos, in which females often transfer

between unit-groups at the time of encounters, relations between groups are an important key to understanding their regional society above the unit-group level. The present paper aims to describe the circumstances in which inter-group encounters occurred, and the social interactions observed within and between groups during encounters.

MATERIALS AND METHODS

In this report, "unit-group" (hereafter abbreviated to "group," unless misleading) refers to a social unit consisting of multiple adult (sexually mature) males, adult females, and their dependent offspring, who consistently share a common home range and generally move together within that range (Kano, 1982; Kitamura, 1983). This is equivalent to the "unit-group" (Nishida, 1968) or "community" (Goodall, 1983) observed in chimpanzees (*Pan troglodytes*), as concluded by Kitamura (1983). Temporary groups formed within unit-groups are referred to as "parties" (Sugiyama, 1969). Parties of bonobos are larger than those of chimpanzees and often of bisexual (or "mixed" [Reynolds, 1965]) composition. An "encounter" was judged to have begun when members of two groups had clearly made visual contact with one another, and to have ended when visual contact was thought to have been broken.

The study was conducted at Wamba (0°10'N, 22°34'E) in Djolu Zone, Tshuapa-Equateur, Republic of Zaire. At Wamba six groups of bonobos (E1, E2, P, B, K, and S) have overlapping home ranges (Fig. 1). In 1988, E1 group consisted of 33 animals, E2 of 54, and P of 39, while B and K, which have not been habituated, were each estimated to consist of about 100 animals (Kano & Mulavwa, 1984). On the basis of fragmentary data, S group is thought to be a large group consisting of more than 100 animals. Of these six groups, E1 and P were the main study groups.

E1 and E2 groups were formed by the fission of E group, which was first provisioned with sugarcane and pineapples and habituated in 1976, when it consisted of 59 animals (Kuroda, 1979; Kano, 1982). In this group two "sub-units" (Kano, 1982; Kuroda, 1982) were recognized; one, consisting of 19 animals, often used the southern half of the group's home range, while the other, consisting of 36 animals, mainly used the northern half. The remaining four animals were young females whose sub-unit membership was unstable (Kuroda, 1982; Kano, 1982).

Both sub-units repeatedly fused and fissioned. When united, they ranged together for periods of a few days to more than a month. In such periods, various affinitive behaviors were frequently observed between members of different sub-units (Kano, 1986). E group continued to show this sub-unit formation until around 1983, when the two sub-units began to fuse less often. Even on the rare occasions when they united, they frequently showed antagonistic behavior towards one another. After 1984, they ceased to fuse altogether. At this point, E group was judged to have divided into two, and the southern group was named "E1 group," and the northern group "E2 group" (Furuichi, 1987).

The members of E1 and E2 groups were largely those who had been members of

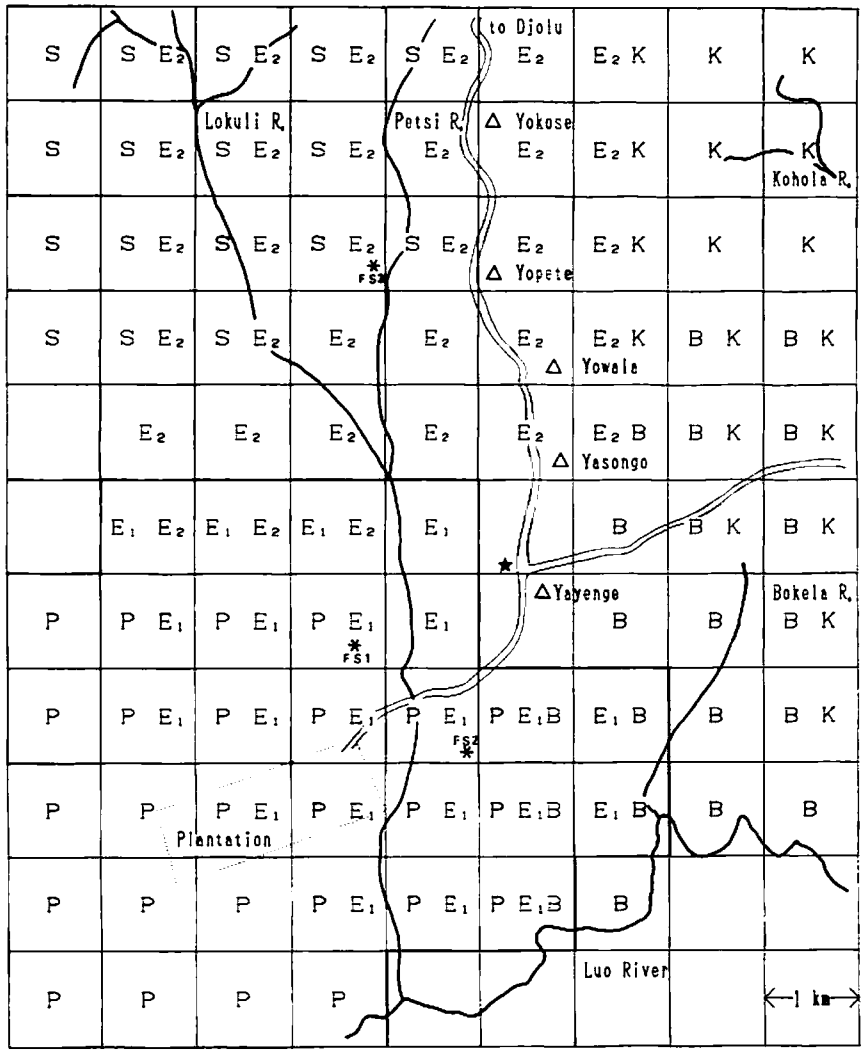

Fig. 1. Home ranges of six unit-groups at Wamba, 1988.
*: feeding sites; △: hamlet of Wamba; ★: base camp.

the southern and northern sub-units, respectively, at the onset of provisioning in 1976. Of the four females whose membership in the sub-units was unstable, two became members of E1 group, and the other two became members of E2 group. They gave birth to offspring and became stable members of their groups. The size of E1 group steadily increased and it comprised 33 animals in early 1988. Known kin relationships in E1 group and fluctuations in its size are shown in Fig. 2.

First attempts to provision P group animals were made in 1978. Although they

approached the feeding sites, they did not enter them. However, in 1986, they began to visit the feeding sites frequently. The group composition and some of the kin relationships among its members have gradually become apparent (Fig. 3).

Observations were made mainly at the three feeding sites located in the Wamba Forest (FS1, FS2, and FS3; Fig. 1). E1 and P groups used mainly FS1 and FS2, while E2 group used FS3.

For age classification, both males and females of more than 15 years were regarded as adults (sexually mature), 7–14 years as adolescents, and less than 6 years as immatures (juveniles and infants; Enomoto, 1990). Parous females were regarded as adults, even if younger than 15 years. Both males and females over 30 years old were categorized as old.

The present study is based on the data obtained in three periods: Period 1

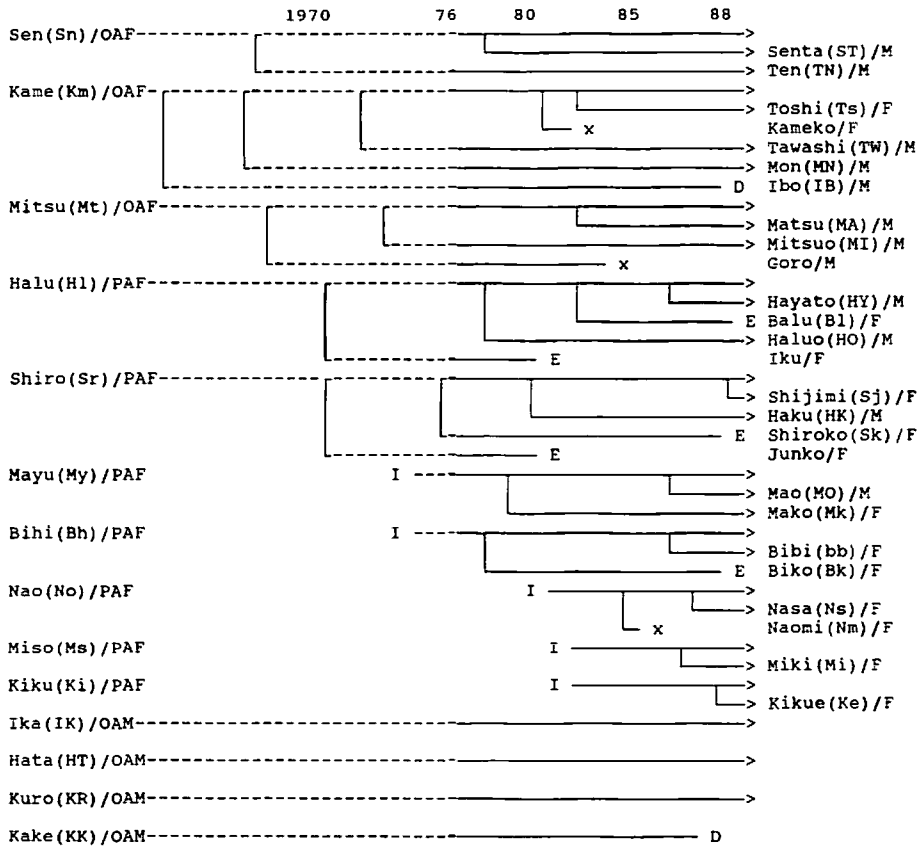

Fig. 2. E1 members.
---: before provisioning: ——: after provisioning; OAF: old adult female; OAM: old adult male; PAF: prime adult female; M: male; F: female; I: immigration; E: emigration; x: died; D: disappeared; ( ): name code.

(November 1984–February 1985), Period II (November 1986–February 1987), and Period III (November 1988–February 1989). The total number of observation days was 284. The total duration of observations was 46,500 min. During Period II, the study period on which the present paper is mainly based, 16,970 min. of observations were made on 115 days. Scan sampling with a 10 min. interval was used for recording spatial distribution of individuals, and *ad libitum* sampling was used to record the behaviors of the bonobos at the feeding sites. The feeding sites measured 50 m in length and 30 m in width, and were partitioned into marked quadrats of 5 m by 5 m.

Names of individuals of E1 group are abbreviated to two letters, and those of P

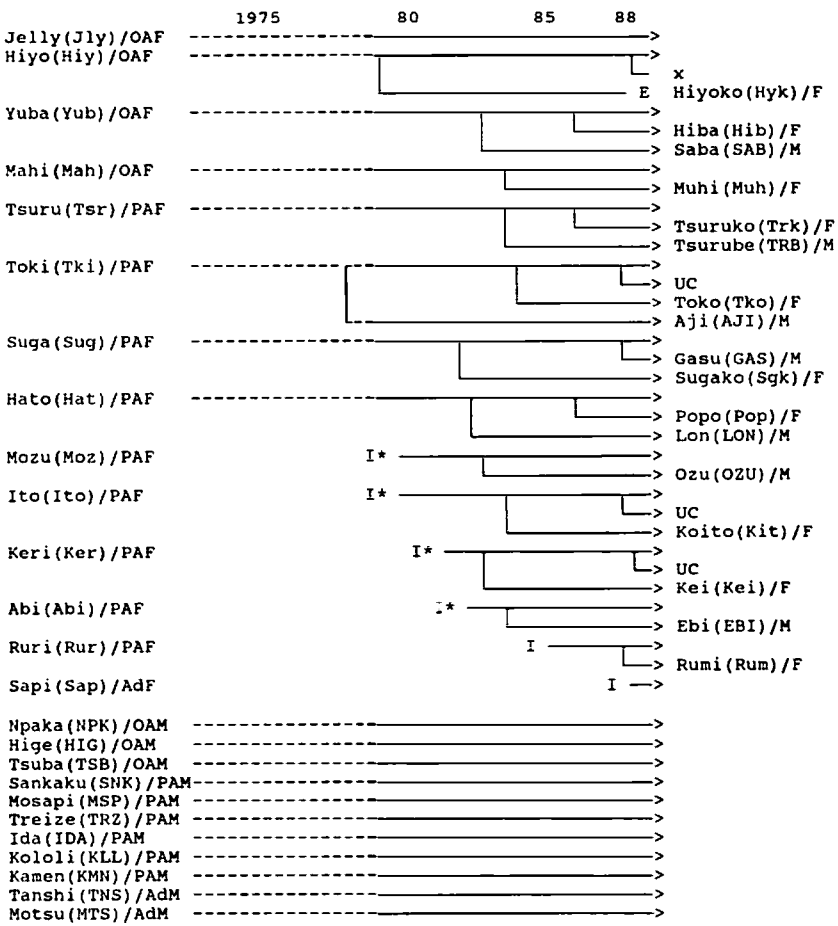

Fig. 3. P members.
---: before provisioning; ——: after provisioning; OAF: old adult female; OAM: old adult male; PAF: prime adult female; PAM: prime adult male; AdF: adolescent female; AdM: adolescent male; F: female; M: male; I: immigration; I*: estimated immigration; E: emigration; x: died; ( ): name code.

group to three. Males are indicated by capital letters alone, while for females the first letter is capital and the other(s) lower case (Fig. 2 and 3).

RESULTS

I. Home Ranges

Changes in the home ranges of E1, E2, and P groups from 1983 to 1986 are shown in Fig. 4. The home ranges of E1 and E2 groups changed drastically after 1984 and P group's home range also shifted. In 1978, before the group divided, E group's home range was about 58 km^2 in area, of which 60–70% overlapped with the home ranges of four neighboring groups (Kano, 1982; Kano & Mulavwa, 1984). The ranges of the southern and northern sub-units of E group overlapped by 80%.

After the division, however, E1 group extended its home range to the southwest and southeast, while E2 group shifted its home range to the north and northwest. In 1986, E1 group's home range was 22 km^2 in area, while E2 group's was 33 km^2, with an overlapping area of only 3 km^2. As E1 group expanded its home range to the southwest, P group came into E1 group's home range to share 15 of the 22 km^2. Also as E1 group expanded its home range to the southeast, it came to share 6 km^2 of its home range with B group, of which 3 km^2 became the common home range of E1, P, and B groups.

Although Fig. 4 shows only 26 km^2 of P group's home range in 1986, it was estimated to 30–40 km^2, as it stretched to the west and where it probably overlapped with the home ranges of some other groups.

II. Types of Inter-Group Encounter

During the study periods, 32 cases of inter-group encounter were directly observed (Table 1). The 25 cases of encounters between E1 and P groups in Period II were all observed at FS1 or FS2, while all the others were observed in natural vegetation.

The encounters can be summarized and categorized into three types by the presence or absence of direct interactions and the antagonistic/affinitive nature of such interactions as follows.

Type a. Groups bark at each other, but no direct interaction occurs. This type of encounter was observed three times [once each between E1 and P groups in Period I, between E1 and B groups in Period II, and between E1 and P groups in Period III].

Case 1. November 24, 1984, 05:58, a party of 13 members of E1 group appeared at FS1. They continued feeding, coming back and forth between FS1 and the forest. 12:58, all disappeared into the forest south of FS1. 13:19, suddenly a noisy bark chorus came from the forest 100 m south of FS1. E1 group members responded with barks. 13:45, the interval of bark exchange became shorter, and the barks noisier. 13:55, 13 members of E1

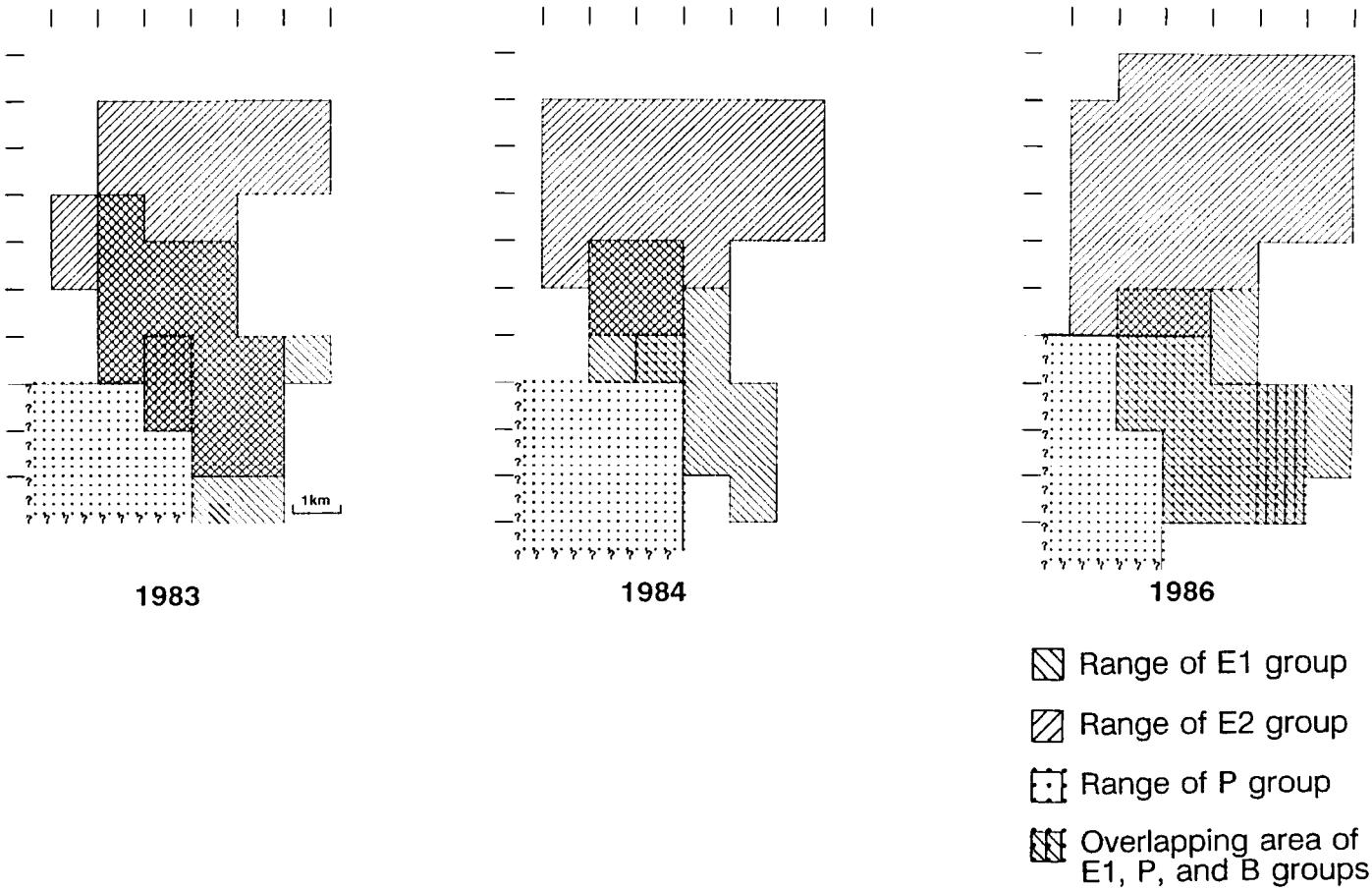

Fig. 4. Changes in the home ranges of E1, E2, and P groups from 1983 to 1986.

Table 1. Party size and group composition in inter-group encounters.

Date (1)		composition of E1 group (2)		Name and composition of unit-group (3)			Encounter type (4)	site (5)	Encounter duration (minutes)	Study Period (6)
		M	F		M	F				
1984 Nov. 24		9	9	P	>20	(?)	a	NH	74	I
1985 Feb. 2		8	9	B	>25	(?)	b	NH	840	I
11		13	15	B	>10	(?)	c	NH	110	I
1986 Dec. 11		15	17	P	8	12	c*	FS1	221	II
12		15	17	P	8	12	c*	FS1	201	II
14		15	17	P	9	11	c	FS1	206	II
22		15	17	B	>25	(?)	a	NH	81	II
24		15	17	P	5	6	c	FS2	373	II
28	⟨1⟩	10	17	P	5	6	c	FS2	148	II
	⟨2⟩	10	17	P	5	6	c	FS2	44	II
30		10	17	P	11	15	c*	FS2	83	II
31	⟨1⟩	10	17	P	10	15	c	FS2	85	II
	⟨2⟩	11	18	P	10	15	c	FS2	30	II
	⟨3⟩	10	17	P	10	15	c	FS2	41	II
1987 Jan. 1		11	17	P	11	16	c	FS2	109	II
3		12	17	P	0	6	c*	FS2	5	II
4	⟨1⟩	12	17	P	8	7	c	FS2	79	II
	⟨2⟩	12	17	P	14	16	c	FS2	149	II
10		12	17	P	13	15	c	FS2	41	II
11		12	17	P	13	15	c	FS2	107	II
12		13	17	P	14	15	c	FS2	29	II
14	⟨1⟩	13	17	P	9	9	c	FS2	97	II
	⟨2⟩	13	17	P	9	8	c*	FS2	54	II
	⟨3⟩	13	17	P	7	8	c*	FS2	49	II
15		13	17	P	9	8	c	FS2	63	II
Feb. 8		10	15	P	16	22	c	FS1	93	II
11		11	15	P	11	18	c	FS1	72	II
12		10	15	P	13	17	c	FS1	40	II
13		11	15	P	11	14	c*	FS1	96	II
1988 Nov. 15		13	19	E2	>25	(?)	c	NH	200	III
17		14	19	E2	>25	(?)	c	NH	145	III
Dec. 15		14	18	P	>20	(?)	a	NH	37	III

(1) ⟨1⟩, ⟨2⟩, or ⟨3⟩: first, second, or third encounter of the day. (2) M: Number of males; F: number of females. (3) >: Estimated total number of individuals, (?): unconfirmed number of males and females. (4) a: Groups bark at each other, but no direct interaction occurs. b: Only antagonistic interactions occur. After the enconter, both groups spend the night nearby, and part the next morning. c: Both groups stay together for a long period of time; after exchanging various types of interactions, they move together for a while or separate. *: Ranging together after an encounter. (5) NH: Natural habitat, FS1: artificial feeding site 1, FS2: artificial feeding site 2. (6) I: November 1984–Feburary 1985; II: November 1986–Feburary 1987; III: November 1988–Feburary 1989.

group and about 20 members of P group were observed at a distance of 10 m in the primary forest south of FS1. They did not intermingle with each other, but only exchanged barks in trees. 14:33, within each group, some animals were grooming. 14:33, E1 group began to move east, emitting loud calls. Although P group members responded with calls, they remained where they were. 15:02, P group began to move south.

In this case no direct social interaction was observed between individuals of the

different groups.

Type b. Only antagonistic interactions occur. After the encounter, both groups spend the night nearby, and part the next morning. This type of encounter was observed only once, between E1 and B groups in Period I.

Case 2. February 2, 1985, 14:05–47, 13 members of E1 group, while feeding at FS2, exchanged barks with B group to the southeast. 16:51, E1 group moved toward B group, while continuing barking. B group responded with barks and approached E1 group. 16:56, the 13 members of E1 group and about 20 members of B group encountered one another at a distance of less than 5 m in the primary forest 400 m southeast of FS2. They barked at each other in the trees. At the rear of E1 group, were *No*, who had recently given birth, and young females (*Ms*, *Ki*); before them were middle-aged and old parous females; and at the front were adult males. 16:59, several males of E1 group (*KK*, *KR*, *IB*, *MO*) chased B group members in the trees with aggressive behaviors, such as beating and pressing down. Old parous females (*Sn*, *Mt*) also chased and charged B group members. 17:12, members of both groups climbed down to the ground and then, after moving 100 m to the south, climbed up into trees again. 17:15, after a sudden chorus of barks, they climbed down to the ground. 17:20, harsh cries were heard, followed by screams. Although there seemed to be a fight on the ground, this was not confirmed by direct observation. 17:27, members of both groups climbed into two stands of *Uapaca guineensis* 20 m apart, and began feeding. The chorus of barks continued. 17:30, several members of B group moved into the stand of *Uapaca* in which E group members were feeding; and a skirmish began between the two groups. 17:50, both groups, while emitting barks, moved 50 m in trees. 17:54, both groups began making beds. Though in different trees, the two groups spent the night at the same place. 06:35, on the next morning, the two groups separated from each other; B group went south, while E1 group to the north.

Type c. Both groups stay together for a long period of time; after exchanging various types of interactions, they move together for a while or separate. This type of encounter was observed 28 times [the case between E1 and B groups in Period I, the two cases between E1 and E2 groups in Period III, and all the 25 cases between E1 and P groups in Period II were encounters of this type].

Case 3. December 11, 1986, 06:10, in the primary forest 200 m north of FS1, E1 and P groups exchanged barks. The distance between the two groups was about 50 m. 06:16, two groups approached each other, until they came into visual contact. The exchange of barks became louder on making contact. 06:47, members of the two groups, while intermingled, slowly began to move toward FS1. 07:05, a male (*IB*) of E1 group copulated with an adolescent female (*Rur*) of P group. 07:36, 32 members of E1 group first appeared at FS1, immediately followed by 20 members of P group. Members of both groups appeared tense. Members of E1 group, who were used to the feeding site, placed themselves at the center, while P group members remained on the periphery. They confronted each other and exchanged barks. 07:50, an adult male (*HIG*) of P group charged at an adult male (*MN*) of E1 group. *MN* avoided the charge, and charged at *HIG*. After a while, *MN* and *HIG* performed rump-rump contact (for descriptions of various "genito-genital contact" behaviors, see Kano, 1980; Kuroda, 1979; Kitamura, 1989), and

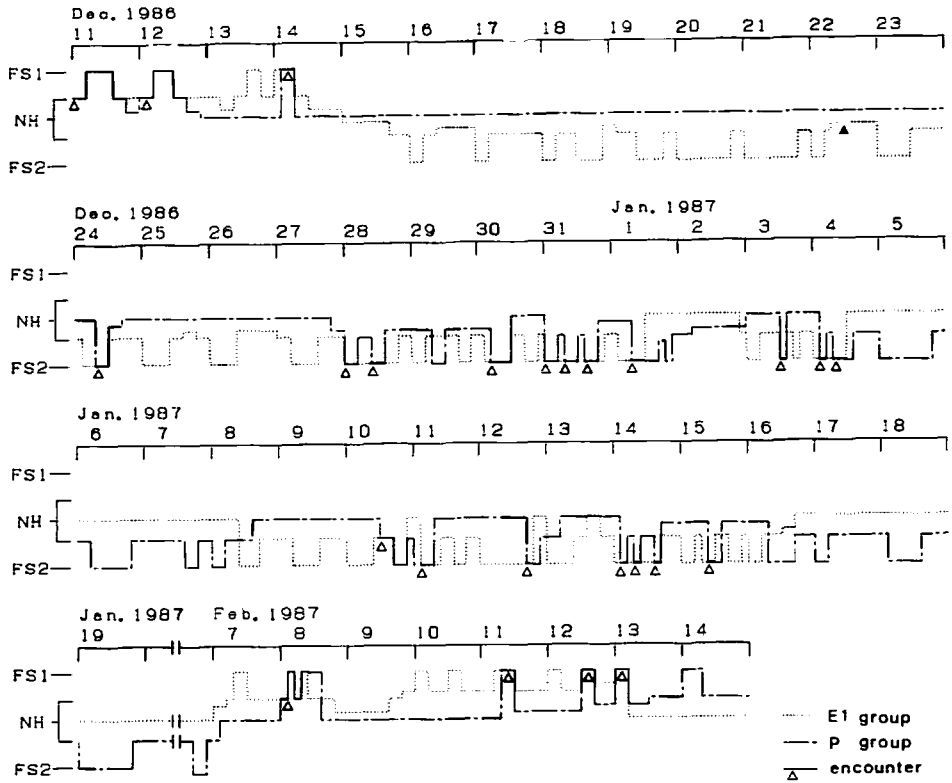

Fig. 5. Ranging patterns of E1 and P groups in 1986.
·····: ranging of E1 group; ——: ranging of P group; —— : encounter; ▲: an encounter between E1 and B groups, NH: natural habitat; FS1: artificial feeding site 1; FS2: artificial feeding site 2.

separated. 07:59, when some P group members attempted to approach the sugarcane, a male (*KK*) of E1 group charged and threatened. The members of P group ran away. 08:11, a female (*Hat*) of P group approached a female (*Sr*) of E1 group, and they performed genito-genital (GG) rubbing. 08:20, a female (*Sn*) of E1 group and an immature male (*LON*, *Hat*'s son) copulated. 08:24, exchange of barks became faint. Members of E1 group began feeding. When a few members of P group attempted to approach the sugarcane placed in the center of the feeding site, males of E1 group charged to threaten them. 08:35, a few adult females of E1 group began feeding together with some members of P group. At this point, the members of P group, who had been watching E1 group feeding, began to move toward the center of the feeding site. After this, no threatening behavior was directed by E1 group toward P group. Members of both groups began feeding together. The tense mood disappeared. After three hours of peaceful co-feeding and resting, both groups moved to the northwest together.

After Case 3, E1 and P groups encountered one another on 25 occasions at FS1 or FS2 on 19 days during the two months until February 1987. Inter-group encounters had never been observed to occur at such a high frequency. The ranging and encounter patterns of the two groups during this period are shown in Fig. 5. In

the first half of this period, when E1 group used FS1, P group also visited FS1, and when E1 group began to use FS2, P group also moved to FS2; and again, in the latter half, when E1 group shifted to use FS1, P group shifted their ranging area to the vicinity of FS1. In other words, P group showed ranging patterns as if to follow E1 group, and there were repeated encounters. After 1988, the frequency of encounter between E1 and P groups decreased, and E1 group began to have encounters with E2 group.

When a group at a feeding site sensed the presence of another, it began a chorus of barks, and gradually the two groups began to exchange barks. In some cases antagonistic interactions occurred, while in some others, the encounter ended simply with the exchange of barks. Either way, tension between the groups rose. However, as time passed, they often came to co-feed or rest peacefully. Often the encounter came to an end when one of the groups left the feeding site. Even when the members of the two groups intermingled in the process, they separated again to form the original groups on leaving. Only in a few cases did the two groups simultaneously begin to move, and travel together. Even then, such co-traveling did not last long, and the groups separated after 1–2 hours. Such patterns of fusion and fission resemble those of parties within groups (Kano, 1986).

During Period II, E1 group comprised 32 animals, and P group 39 animals. The mean group size during inter-group encounters was 28.8 (25–32, n=25) for E1 group and 21.8 (6–38, n=25) for P group. Although one case was recorded of an encounter between an all-female party of six (three mothers and their female offspring) from P group, and a bisexual party from E1 group, in all other cases the encounter was between bisexual parties (E1 group, 100%; P group, 96%; see Table 1).

In the breakdown of the observed inter-group encounters by the above types (Table 1), it is notable that type c was prominent in feeding site situations, while not so in natural vegetation (Fisher's exact test, $p=<0.01$, one-tailed). However, care should be taken in interpreting this tendency, because type a and b encounters are noisier than type c encounters, and so are more easily monitored in natural conditions. Moreover, it should be noted that type c encounters, i.e. friendly ones, were indeed recorded in natural conditions.

III. Temporary Transfers of Adolescent Females

During encounters in natural vegetation, temporary transfers of adolescent females were observed between E1 and B groups in Period I, and between E1 and E2 groups in Period III. The E1–B case occurred when 28 members of E1 group and about 10 members of B group encountered one another on the western periphery of E1 group's home range, which overlapped with B group's home range. Immediately after the encounter, the two groups only confronted and barked at each other. As time passed, they calmed down a little, and three GG rubbings and two copulations were observed between members of different groups. All bonobos present then began to feed on young leaves of two trees 30–40 m apart (one *Brachystegia laulentii* and the other *Guibourtia demeusei*, both Caesalpiniaceae), with members of both groups feeding together in each tree. B group began moving south 110 min. later, and the encounter came to an end. An

adolescent female, who had not been observed before, was identified in E1 group. Between her and *Sk* [E1], three GG rubbings were performed in series. Shortly after this, most females of E1 group joined in an intensive attack on her. She ran around screaming, and eventually left to the south, in the direction that B group had left. Although the reason for the attack is unknown, it is certain that a temporary inter-group transfer had occurred.

When the E1 and E2 had two encounters on November 15 and 17, 1988, with a total duration of 345 min., transfer was recorded once on November 17. An adolescent female, *Shiwa* (estimated to be 8–9 years old), who had been identified in E2 group, was observed in E1 group when the latter began moving after encounter. She was observed to be together with E1 group until November 28, although she disappeared thereafter (perhaps transferred to another group).

IV. Spacing of Individuals at Feeding Sites

Table 2 shows the mean inter-individual distances observed during encounters between E1 and P groups during Period II, recorded in scans at 10 min. interval. The scans were taken only after a while when the initial excitement of the encounter had abated. Also four individuals (*Tsr*, *Ker*, *Abi*, and *KMN*), who were rarely involved in the encounters, were omitted from the analysis.

While some of the inter-group male-female and female-female distances were around 10 m or even less (underlined in Table 2), most of the inter-group male-male distances were greater than 10 m. In other words, male-female and female-female proximity was common between the two groups; they intermingled and frequently exchanged various social interactions. By contrast, males kept a certain distance from the males of the other group; few instances of approach, co-feeding, or side-by-side resting were recorded. During encounters, the average distance between males of different groups was 18.6 m, compared with 15.6 m for females, and 17.8 m for males and females. Of these, the average distance between females of different groups was the shortest, although the difference in the mean distance between females of different groups was not statistically significant in comparison with males of different groups (Table 2; $t=1.99$, $df=17$, $p>0.01$).

During inter-group encounters, distances between individuals of the same groups were less than those between individuals of different groups (Tables 3a and 3b). This tendency was the same in both groups. The average distance between E1 males was 13.9 m, 14.1 m for between E1 females, 15.4 m for between E1 males and females, 11.7 m for between P males, 14.6 m for between P females, and 12.6 m for between P males and females. When members of one group visited a feeding site alone, prime and older parous females, their sons, and relatively high-ranking males occupied the central part of the site, while young parous females and low-ranking males occupied the periphery. Also young nulliparous females usually associated with their respective "specific senior females" (SSF; Furuichi, 1989; Idani, in press); for example, *Ki* approached *Hl*, and *Rur* approached *Tki*. During inter-group encounters, however, such approaches by young nulliparous females to SSFs were not observed. Rather they spent more time with members of the other group.

Table 2. Average distance (m) between individuals of E1 and P groups.

		E1 group males										E1 group females										
		KK	IK	HT	KR	IB	MN	TN	TW	MO	HO	Sn	Km	Mt	Hl	Sr	Bh	My	No	Ms	Ki	Sk
P males	NPK	*	19.3	20.3	20.2	16.0	10.8	16.2	14.3	*	23.6	19.9	16.3	16.0	*	24.0	21.9	9.3	16.2	26.6	14.4	13.9
	HIG	*	19.6	22.1	20.6	24.4	16.6	14.3	15.9	*	11.8	12.6	18.0	13.0	21.6	14.7	22.0	17.2	19.7	23.7	22.1	12.9
	TSB	*	16.1	17.7	19.3	21.8	14.7	12.3	17.8	*	16.6	16.4	20.9	13.0	20.1	15.4	26.5	23.9	10.8	21.2	11.9	17.8
	SNK	*	18.7	18.2	20.0	17.6	20.3	16.9	21.3	*	20.0	17.3	22.7	12.7	17.3	17.9	25.2	23.8	11.9	22.5	10.9	16.5
	MSP	*	19.7	26.4	25.4	18.1	17.2	15.7	20.4	*	16.1	15.3	23.0	15.0	20.5	15.1	23.0	26.4	14.4	24.3	14.4	10.8
	TRZ	*	18.2	21.2	16.3	12.0	11.5	15.4	12.8	*	20.4	18.6	17.9	17.1	25.4	21.2	27.5	13.9	12.1	21.7	13.8	14.3
	IDA	*	23.2	28.1	25.2	22.6	20.3	17.7	18.1	*	13.8	16.3	20.5	16.8	23.9	17.4	17.8	20.6	22.6	22.0	22.0	17.3
	KLL	*	17.8	24.1	21.0	17.8	14.2	11.0	21.5	*	16.7	12.0	21.5	14.6	21.2	23.1	25.2	28.9	8.4	23.0	3.1	16.1
	TNS	*	26.3	13.7	23.5	20.6	23.5	15.4	34.6	*	16.9	19.6	19.5	16.6	17.6	13.4	19.0	37.5	12.8	26.3	7.1	17.7
	MTS	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
	AJI	*	17.2	25.8	20.4	18.5	11.8	13.4	13.0	*	8.3	7.1	18.9	17.8	*	12.9	13.0	9.4	16.9	20.7	15.6	7.3
Total avarage			19.6	21.8	21.2	18.9	16.6	14.8	19.3	*	16.4	15.5	19.9	15.3	21.0	17.5	22.1	21.1	14.6	23.2	13.5	14.5
P females	Jly	*	21.1	26.0	19.5	23.3	17.5	13.0	11.7	*	12.8	12.6	15.7	12.1	*	17.3	14.1	14.9	11.4	22.5	*	11.0
	Hiy	*	26.0	27.1	18.8	*	*	*	18.6	*	14.6	21.8	23.1	13.7	16.0	17.9	24.0	24.2	*	*	*	15.3
	Yub	*	18.9	20.1	12.7	*	21.0	18.8	9.8	*	15.2	21.5	16.8	9.6	16.3	16.4	17.4	14.0	3.2	*	*	12.9
	Mah	*	18.4	*	20.9	25.4	30.3	21.6	32.6	*	25.1	*	29.3	*	*	22.8	17.1	30.0	*	16.3	*	24.1
	Tki	*	23.4	26.3	21.3	20.6	20.7	13.2	18.3	*	16.9	13.7	18.3	18.5	27.5	20.1	22.0	17.0	24.4	21.2	28.5	14.0
	Sug	*	8.9	8.3	14.3	24.2	16.0	9.5	23.0	*	14.3	6.8	18.4	8.6	8.1	12.6	19.6	26.9	5.3	17.6	4.5	17.0
	Hat	*	24.0	21.3	21.0	4.3	19.6	10.0	17.5	*	16.6	13.2	21.6	7.3	15.3	16.2	19.8	18.9	10.5	21.4	3.4	17.1
	Moz	*	9.3	5.4	20.9	14.9	20.9	11.7	*	*	14.3	14.5	17.8	13.3	11.1	6.5	21.2	31.7	13.2	20.0	*	5.1
	Ito	*	18.5	19.6	18.8	19.6	17.5	15.4	17.0	*	12.8	15.6	17.3	18.3	17.9	16.0	19.6	14.8	18.7	23.8	*	7.1
	Rur	*	10.8	14.7	17.0	19.8	16.4	12.1	17.9	*	10.5	4.8	21.8	11.2	3.6	11.7	14.1	21.2	4.4	17.6	5.1	14.2
	Hyk	*	15.4	*	13.4	13.1	14.3	*	*	*	16.8	*	11.9	*	*	11.3	16.0	*	*	*	*	*
Total avarage		*	17.7	18.8	18.1	18.4	19.4	13.9	18.5	*	15.4	13.8	19.3	12.5	14.5	15.3	18.6	21.4	11.4	20.1	10.4	13.8

* incalculable; underlined: within 10 m.

Table 3a. Average distance (m) between E1 members in encounters with P group.

	Males										Females										
	KK	IK	HT	KR	IB	MN	TN	TW	MO	HO	Sn	Km	Mt	Hl	Sr	Bh	My	No	Ms	Ki	Sk
KK	—	*	*	*	*	*	28.7	*	27.2	*	24.3	22.8	*	*	*	*	*	*	*	*	*
IK		—	9.9	9.4	16.9	10.2	9.2	17.6	*	14.2	15.2	12.1	14.1	12.6	14.9	15.3	18.9	8.6	13.4	11.4	16.2
HT			—	10.2	14.4	10.9	12.6	14.3	*	15.6	23.3	13.7	18.4	12.0	16.6	16.4	18.8	9.5	11.8	13.8	21.0
KR				—	12.1	11.6	11.0	11.5	*	11.3	21.7	8.6	16.8	15.0	15.7	20.4	14.6	12.4	13.3	18.0	18.4
IB					—	11.1	15.5	9.9	*	16.1	17.9	14.3	18.4	24.1	18.9	20.8	20.4	20.7	18.6	19.6	20.7
MN						—	10.8	11.9	*	13.6	15.2	12.2	13.8	19.4	14.7	18.2	14.4	10.7	13.8	13.4	13.3
TN							—	16.0	25.8	14.2	10.4	10.1	8.4	9.9	14.4	17.8	17.7	9.0	15.6	9.6	12.9
TW								—	*	9.6	23.8	8.3	14.8	22.4	16.2	13.4	9.0	14.7	22.9	17.0	13.2
MO									—	*	*	*	20.2	*	*	*	*	23.1	*	22.6	*
HO										—	16.2	7.9	12.6	13.9	7.6	9.9	13.4	10.2	17.0	12.4	14.3
Sn											—	23.3	11.5	9.2	17.2	19.3	25.3	8.3	14.8	6.4	18.8
Km												—	13.4	15.3	13.9	11.4	9.4	13.3	17.7	15.5	13.3
Mt													—	9.8	12.7	15.8	17.4	5.6	18.1	5.5	12.2
Hl														—	12.3	14.3	24.1	10.5	19.2	7.5	16.5
Sr															—	12.3	16.8	9.1	14.8	14.3	12.3
Bh																—	17.2	16.9	17.2	14.4	14.8
My																	—	20.6	15.7	18.4	6.7
No																		—	12.5	4.3	16.5
Ms																			—	12.4	13.9
Ki																				—	14.5
Sk																					—

* incalculable

Table 3b. Average distance (m) between P members in encounters with E1 group.

	Males											Females										
	NPK	HIG	TSB	SNK	MSP	TRZ	IDA	KLL	TNS	MTS	AJI	Jly	Hiy	Yub	Mah	Tki	Sug	Hat	Moz	Ito	Rur	Hyk
NPK	—	15.2	12.2	12.7	9.5	6.1	20.5	8.5	*	*	*	6.0	*	*	*	19.8	17.4	*	*	10.0	14.6	*
HIG		—	15.5	12.1	13.3	14.4	9.0	16.6	5.7	*	9.4	7.7	14.4	13.5	*	7.5	23.5	12.0	6.7	5.7	24.5	*
TSB			—	10.4	11.6	13.2	15.5	8.1	10.8	*	10.0	8.1	15.3	13.4	*	22.1	9.6	8.8	3.4	9.6	7.8	*
SNK				—	12.7	15.1	17.6	11.2	11.4	*	9.4	4.6	16.2	14.3	*	23.0	11.4	8.2	10.2	13.4	10.2	14.4
MSP					—	13.8	13.3	8.9	3.5	*	12.5	8.2	15.8	19.6	*	17.5	15.8	16.7	9.7	9.2	15.6	*
TRZ						—	16.1	12.9	11.1	*	7.8	7.7	17.3	11.7	*	16.5	17.2	13.8	8.8	8.5	13.3	5.7
IDA							—	19.9	10.6	*	12.8	13.0	16.0	16.1	13.9	5.7	25.3	15.9	3.5	8.9	26.9	*
KLL								—	3.3	*	9.6	4.3	22.5	21.9	*	21.7	7.5	15.6	7.2	8.7	6.7	*
TNS									—	*	*	*	*	*	*	*	*	10.8	10.5	7.7	*	11.2
MTS										—	*	*	*	*	*	*	*	*	*	*	*	*
AJI											—	5.8	*	*	*	10.6	18.2	*	*	5.9	12.3	*
Jly												—	*	*	*	10.4	16.1	*	*	13.6	10.5	*
Hiy													—	15.2	*	12.8	*	11.6	*	*	*	*
Yub														—	*	22.0	*	12.3	*	15.8	*	29.4
Mah															—	13.3	*	*	*	*	29.4	*
Tki																—	*	24.7	*	9.5	26.0	*
Sug																	—	8.2	3.3	17.6	5.6	*
Hat																		—	7.9	18.5	*	*
Moz																			—	6.7	*	*
Ito																				—	11.2	*
Rur																					—	*
Hyk																						—

* incalculable

Table 4. Proximity between E1 and P groups.

E1 group			Number of observations		OUs of proximity within 5 m with P members (%)	
			Of all 25 encounters	Of all 270 observation units (OUs)	Male	Female
Female	OA	Sn	23	264	39	39
		Km	21	257	5	8
		Mt	23	239	21	42
	PA	Hl	23	264	11	55
		Sr	25	269	22	22
		Bh	25	269	0	10
		My	24	262	7	15
		No	23	261	22	78
		Ms	25	269	0	11
	Ad	Ki	21	253	56	78
		Sk	25	269	0	8
Male	OA	KK	6	100	0	0
		IK	24	262	0	17
		HT	23	264	0	14
		KR	19	209	6	0
	PA	IB	17	211	0	11
		MN	22	239	14	29
		TN	19	226	7	43
	Ad	TW	10	150	22	5
		MO	5	113	0	0
		HO	25	269	0	15

P group			Number of observations		OUs of proximity within 5 m with E1 members (%)	
			Of all 25 encounters	Of all 270 observation units (OUs)	Male	Female
Female	OA	Jly	13	140	8	33
		Hiy	12	189	0	0
		Yub	13	121	6	17
		Mah	17	204	0	0
		Tsr	4	30	0	0
	PA	Tki	12	104	0	22
		Sug	23	255	58	83
		Hat	17	165	17	67
		Moz	13	117	0	50
		Ito	23	203	9	17
		Ker	3	20	0	0
		Abi	2	13	0	0
	Ad	Rur	19	181	43	71
		Hyk	19	203	0	0
Male	OA	NPK	19	208	18	9
		HIG	20	223	7	38
		TSB	23	211	14	21
	PA	SNK	16	127	0	0
		MSP	23	243	6	40
		TRZ	20	216	13	40
		IDA	16	116	0	27
		KLL	14	100	18	55
		KMN	2	11	0	0
	Ad	TNS	15	156	0	0
		MTS	9	130	0	0
		AJI	10	115	0	17

OA: Old adult, PA: prime adult, Ad: adolescent.

For the 2,700 min. that E1 and P groups were observed together at the feeding sites, scans were taken at 10 min. intervals to record all individuals within 5 m of one another. Young nulliparous females (*Ki* and *Rur*) and an adult female without dependent offspring (*No*) showed high proximity frequencies (Table 4). They frequently approached parous females of the other group, when feeding or resting. Young nulliparous females, *Ki* and *Rur* in particular, also approached males of the other group. Among the parous females, *Hl* and *Sug* showed most frequent proximity to females of the other group. *Sug* showed a particularly high proximity not only to females, but also to males of the other group. During this period *Sug* (with *Sgk*, her dependent female offspring) was observed to join E1 group temporarily, and to move with them, on six occasions. However, she returned to P group after one or two days at the most. Although males showed relatively high proximity frequencies with females of the other group, their proximity frequencies with the males of the other group were low. Among males, the alpha males (*TN* and *KLL*) had the most frequent inter-group proximity with females.

V. Interactions of Females

Social interactions observed between females of E1 and P groups were GG rubbing, grooming, begging for food, peering, play and aggression. Of these, begging for food was observed only twice and was from juveniles to adults; and play only three times between juveniles.

Occurrences of inter-group GG rubbing were remarkably frequent during the first 30 min. after the encounter had begun, and then sharply declined in frequency as time passed (Fig. 6). When only one group visited a feeding site, the frequency of intra-group GG rubbing was remarkably high during the first 15 min. after the group had entered the feeding site. The frequency of GG rubbing during encounters showed a higher value between females of different groups than within groups (Table 5; Fig. 7).

There were also differences between individuals, of the same age class in the frequency of GG rubbing. The 26 cases of inter-group GG rubbing observed were performed between eight females of E1 group and five females of P group. In E1 group, *No* had the highest frequency of inter-group GG rubbing, though it was not significantly greater than others ($\chi^2=2.53$, $df=1$, $p>0.05$). In P group, *Sug* had the highest frequency of inter-group GG rubbing (Table 5: $\chi^2=17.69$, $df=1$, $p<0.01$). Although young nulliparous females, such as *Ki* and *Rur*, seldom performed inter-group GG rubbing, they had the highest frequencies of intra-group GG rubbing (Fig. 7).

A period of grooming between a pair of individuals, when it was separated by no intervals of one minute or more, was counted as a single grooming session, irrespective of which animal was the groomer. When two grooming individuals were joined by another, and the grooming was continued by the three, the first grooming session by the two was treated separately from the second grooming session by the three.

Six grooming sessions were recorded between females of different groups, involving five individuals (*Sn*, *Mt*, *No*, *Sug*, and *Hat*). These grooming sessions ended

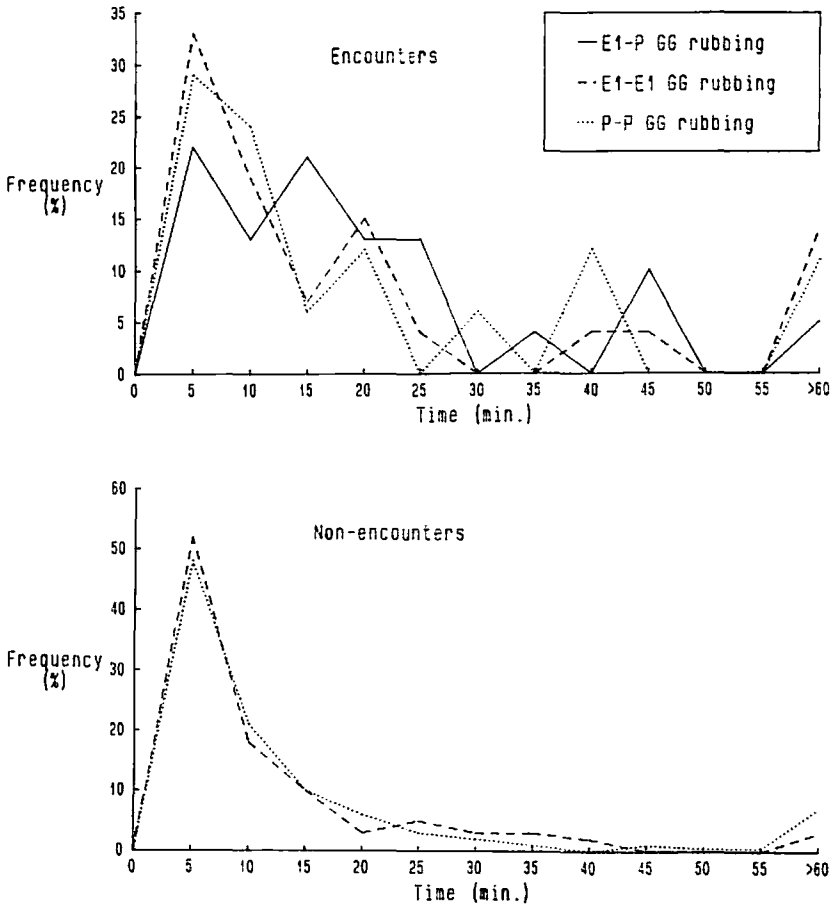

Fig. 6. Changes in inter- and intra-group GG rubbing at feeding sites. >60: Over 60 minutes. For E1–P copulations during encounters, the time scale starts from the GG rubbing of encounters, and for E1–E1 or P–P GG rubbing in non-enounter contexts, it starts from the entry into the feeding sites.

within 3 min. (47–178 sec.), with one exception (*Mt–Sug*, 38 min.). Of intra-group grooming, 17 sessions were recorded in E1 group, and 11 in P group. Of these, eight (47%) sessions in E1 group and six (64%) sessions in P group were between mothers and their offspring. If these are excluded, the incidence of intra-group grooming sessions was 0.0054 times/animal/hr for E1 group and 0.0024 times/animal/hr for P group, slightly greater than the incidence of inter-group grooming sessions, 0.0016 times/animal/hr.

Neither intra- nor inter-group grooming occurred immediately after entering the feeding site, but about 1 hr later (Fig. 8).

The incidence of peering between females of different groups was 12 cases (0.26 + 0.13 = 0.39 times/hr), while that within either group was seven cases (0.23 times/hr; Fig. 9). Peering behaviors often occurred during the excited period im-

Table 5. Number of genito-genital rubbing between females of each group during encounters between E1 and P groups.

E1 Females	OA			PA						Ad
	Sn	*Km*	*Mt*	*Hl*	*Sr*	*Bh*	*My*	*No*	*Ms*	*Ki*
Inter-group	4	1	4	5	3	1	0	7	0	1
Intra-group	4	3	3	7	2	3	1	4	2	7
Total	8	4	7	12	5	4	1	11	2	8
P Females	OA			PA						Ad
	Jly	*Hiy*	*Yub*	*Mah*	*Tki*	*Sug*	*Hat*	*Moz*	*Ito*	*Rur*
Inter-group	0	1	5	0	0	15	3	0	0	1
Intra-group	1	0	2	1	3	2	2	0	0	4
Total	1	1	7	1	3	17	5	0	0	5

OA: old adult; PA: prime adult; Ad: adolescent.

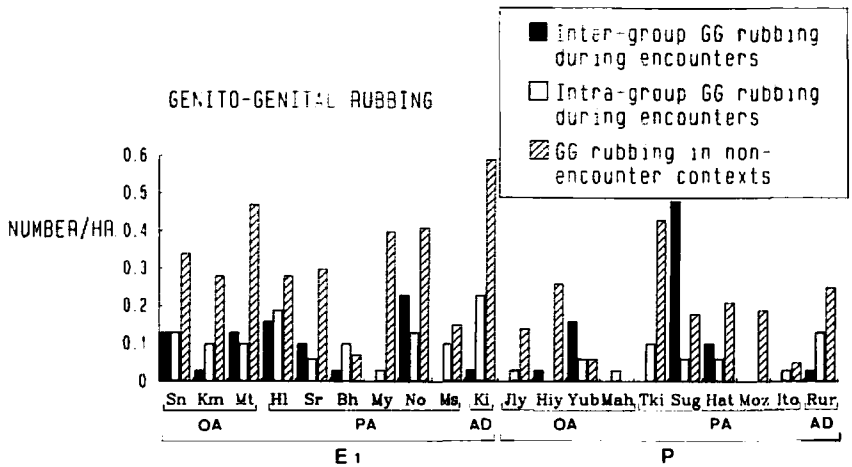

Fig. 7. Frequency of genito-genital rubbing between females of each group during encounters between E1 and P groups.

mediately after an encounter had begun. Although there was one case in which aggression followed peering, in most cases one individual approached another and peered into the face or hand, then the former sat near the latter, or simply left the spot. In two cases, GG rubbing followed peering.

Between females of different groups, aggressive interactions were recorded three times. In the first case, the interaction occurred when *Sug* forcibly attempted to take a stick of sugarcane away from *Bh*. *Sug* held *Bh*'s sugarcane with one hand and slapped *Bh* with the other. *Bh* did not give up the sugarcane, but took it back from *Sug*'s hand, and left the spot with screams. In the second case, *Ito* was embroiled in intra-group fighting in E1 group. She was charged at by *Km* and *Mt*, both old females of E1 group. *Ito* crouched and grimaced, and then ran away with screams. In the third case, *Mt*, on appearing at the feeding site, charged with branch-dragging at *Sug*, who was feeding. *Sug* cried, but remained at the spot. *Mt* rushed to pass her, and sat 15 m away from her.

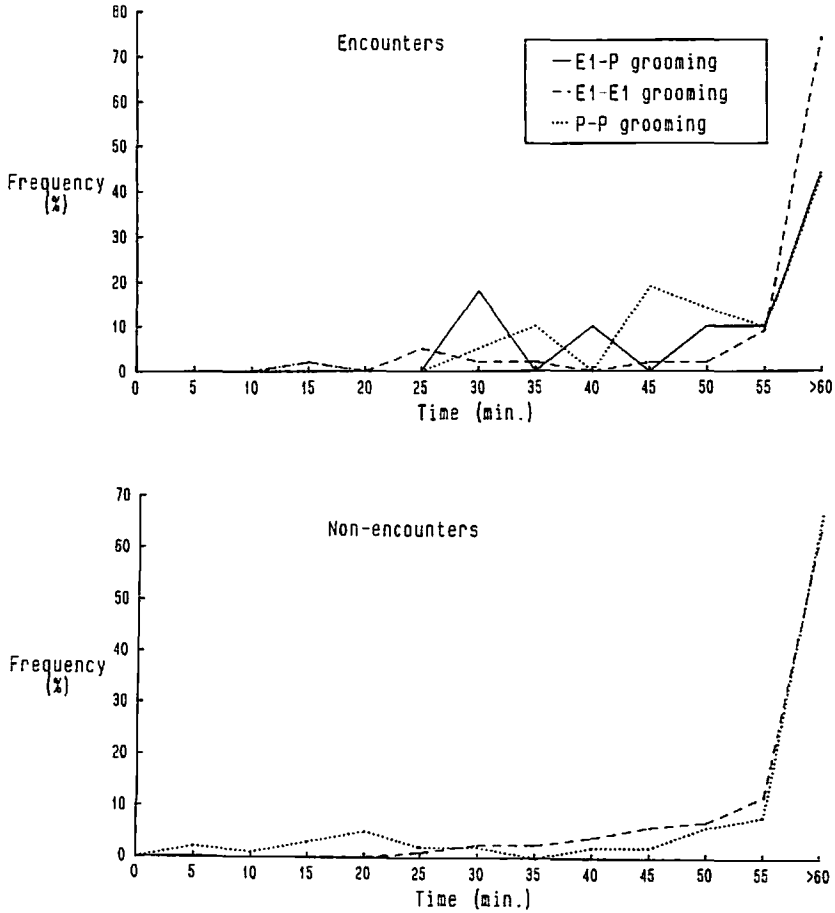

Fig. 8. Changes in inter- and intra-group social grooming at feeding sites. >60: Over 60 minutes. For E1–P begging during encounters, the time scale starts from the social grooming of encounters, and for E1–E1 or P–P social grooming in non-encounter contexts, it starts from the entry into the feeding sites.

Between females within groups, aggressive interactions were recorded seven times in E1 group and four times in P group. In E1 group, *Hl* was the aggressor in five cases, of which *My* was the aggressee in four, and *Bh* was the aggressee in one. *Hl* gave a "bite," which is a rather rough expression of aggression, in two cases to *My* and one case to *Bh*; in both cases, the aggressee reacted with repeated rolling over on the spot, as if in a temper-tantrum. Two cases were simple chase-and-run. The remaining two cases observed in E1 group were threats (*Sn* to *Bl*, and *Bh* to *Mk*). All four aggressive intra-group female interactions in P group were threats (*Sug* to *Hat*, *Hat* to *Moz*, *Tki* to *Moz*, and *Hiy* to *Rur*).

GG rubbing and grooming were also observed between females of E1 and other groups (E1–B in Period I; E1–E2 in natural vegetation in Period III). In these social interactions, although *Sn*, *Mt*, *Hl*, *Bh*, *No*, *Sk* were known to be involved,

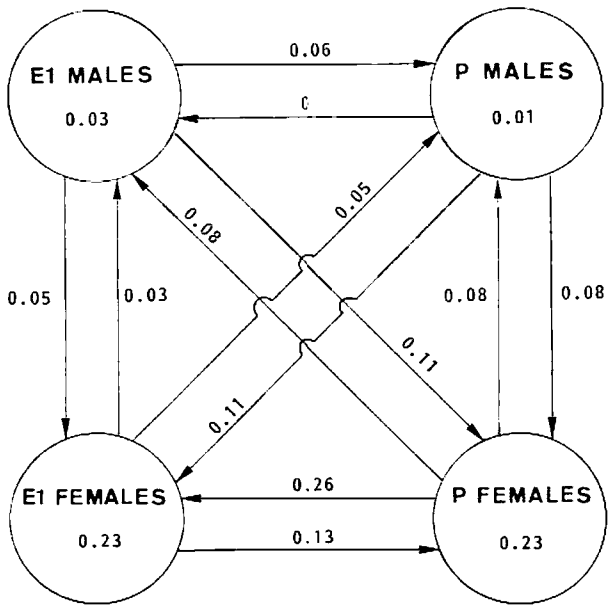

Fig. 9. Peering behavior (frequency per hour) between E1 and P unit-groups. Numbers within circles show the frequency between the same sex in a group.

the females of the other groups could not be identified.

VI. Interactions of Males

Although proximity between males of different groups was rarely observed, there were frequently aggressive interactions when they approached. The incidence of aggressive interactions between males was greater than that between any other combination of age-sex classes (Table 6). Of all 113 aggressive interactions, 62 cases occurred between males. Occurrences of aggressive behavior showed a marked concentration just after the encounter had begun, and sharply declined in frequency as time passed (Fig. 10).

Between males of E1 and P groups, 29 cases of aggressive interactions were recorded (21 from E1 group to P group; 8 from P to E1). Of the eight cases of aggression from P group to E1 group, *KLL*, the alpha male of P group, participated in five (62.5%). By contrast, in aggression from E1 group to P group, *TN*, the alpha male of E1 group, who most frequently showed intra-group aggression, did not participate at all, while *HT*, a low-ranking male, who was always attacked in intra-group aggression, most frequently charged at males of P group. *HT* participated in nine (43%) cases. There was no particular individual in either group who was most often attacked.

In inter-group aggressive interactions, behaviors such as charging, mock charge, chase, and threat were often observed, while behaviors involving direct bodily

Table 6. Aggressive interactions between age-sex classes of E1 and P groups.

			Aggressor							
			E1 group				P group			
			PAM	AdM	PAF	AdF	PAM	AdM	PAF	AdF
Aggressee	E1 group	PAM	18(16)	0	1(1)	1	5(1)	0	1	0
		AdM	5(2)	1	3	0	3	0	0	0
		PAF	6(4)	0	5	0	2	0	1	0
		AdF	4(2)	2	2	0	1	0	0	0
	P group	PAM	16(1)	3(2)	2	3	8(7)	0	1	0
		AdM	1	1	0	0	1(1)	0	1	1
		PAF	3	0	2	0	1	0	3	0
		AdF	1	0	0	0	2	1	1	0

PAM: prime adult male; AdM: adolescent male; PAF: prime adult female; AdF: adolescent female; ( ): number of mounting or rump contact after the aggressive interaction.

contact, such as biting, beating, kicking, and pressing were rare. Of submissive behavior patterns such as running away, evasion, grimace, and crouching were seen. Most aggressive interactions were one-to-one. Cooperative attacks by two or more individuals were rare. In short, most aggressive interactions took the following pattern: The aggressor approaches, feints against, threatens, or mock-charges at the aggressee, while the aggressee evades or runs away. Such interactions rarely developed into fierce fighting. Appeasement or assurance behaviors such as mounting and rump-rump contact, which were common in intra-group aggressions, rarely occurred (Table 6). For example, when the aggressee crouched with grimace, and showed submission by presenting the rear part to the aggressor, the latter often ignored the former's reaction and went away.

Males rarely showed affinitive social behavior such as grooming toward males of the other group during inter-group encounters. *TW*, a young male of E1 group, showed peering toward *TRZ* of P group four times. In two cases, when *TW* peered at *TRZ*, an aggressive interaction occurred, *TW* mounted *TRZ*, and after *TW* peered at *TRZ* again, they parted. In the remaining two cases, *TW* peered at *TRZ*, who was feeding. *TRZ* ignored *TW* and continued feeding, and *TW* soon left.

VII. Inter-Group Interactions between Males and Females

The most prominent inter-group interactions between males and females were copulations. In the encounters between E1 and P groups at the feeding sites during Period II, 53% of all inter-group copulations occurred within the first 15 min. after the encounter had begun (Fig. 11). By comparison, intra-group copulations was most frequent during the first 10 min. after the entry into the feeding site. In other words, copulations occurred immediately after the initial antagonistic interactions in either group, when all individuals were still excited. However, inter-group copulations had longer durations than intra-group copulations. Copulations were also observed in other situations such as when feeding or resting.

Case 4. December 12, 1986, 08:32, *Rur*, an adolescent female of P group, came into FS1 from the forest to the west, looking for sugarcane, but all had been taken, and she got

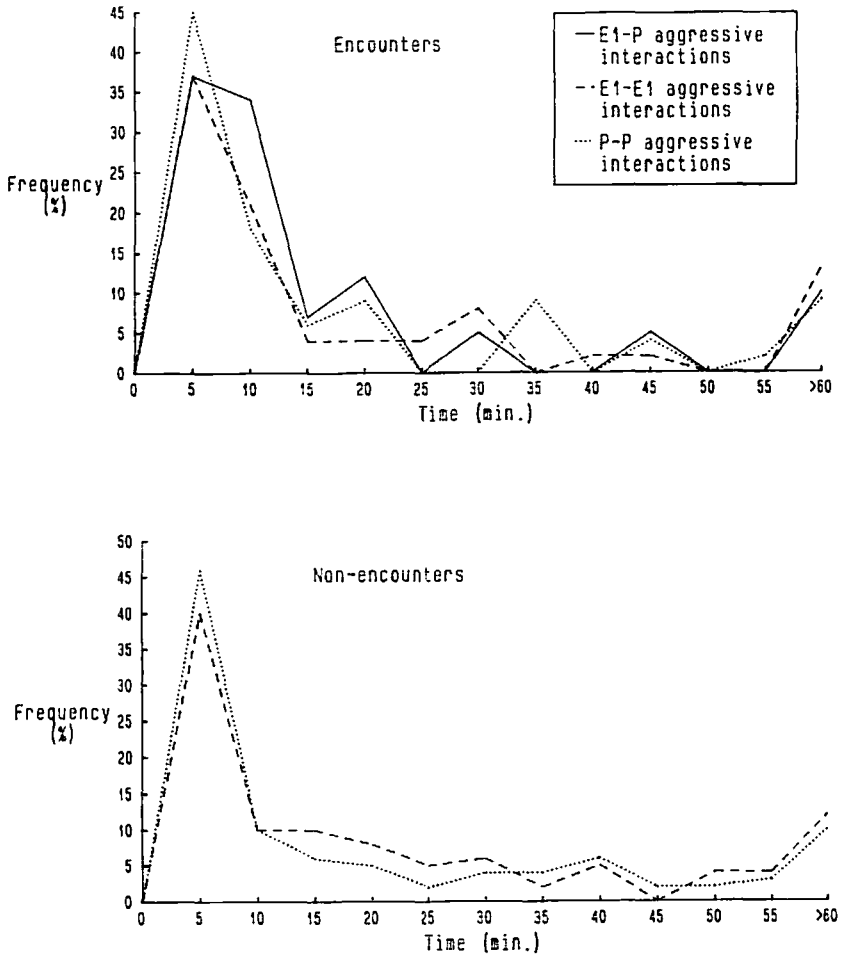

Fig. 10. Changes in inter- and intra-group aggressive behaviors at feeding sites. >60: Over 60 minutes. For E1–P copulations during encounters, the time scale starts from the aggressive behaviors of encounters, and for E1–E1 or P–P aggressive behaviors in non-encounter contexts, it starts from the entry into the feeding sites.

none. 08:34, *Rur* approached two adult males of E1 group, *TN* and *MN*, who were feeding in the center of the feeding site, side by side. She peered at *TN* a little, and presented her rear to him. *TN* stood upright with sugarcane in his hands, and copulated with her. He stopped copulating in 6 sec., and sat to continue feeding. *Rur* approached *MN* sitting 2 m away, and presented to him. 08:35, *MN*, keeping sugarcane in his hands, copulated with her for 25 sec. After copulation, *Rur* snatched a piece of sugarcane from him, and quickly entered the forest to the west. *MN* remained at the spot, and continued feeding.

Case 5. January 12, 1987, 06:46, *Sug* (female, P) and *No* (female, E1) came into FS2

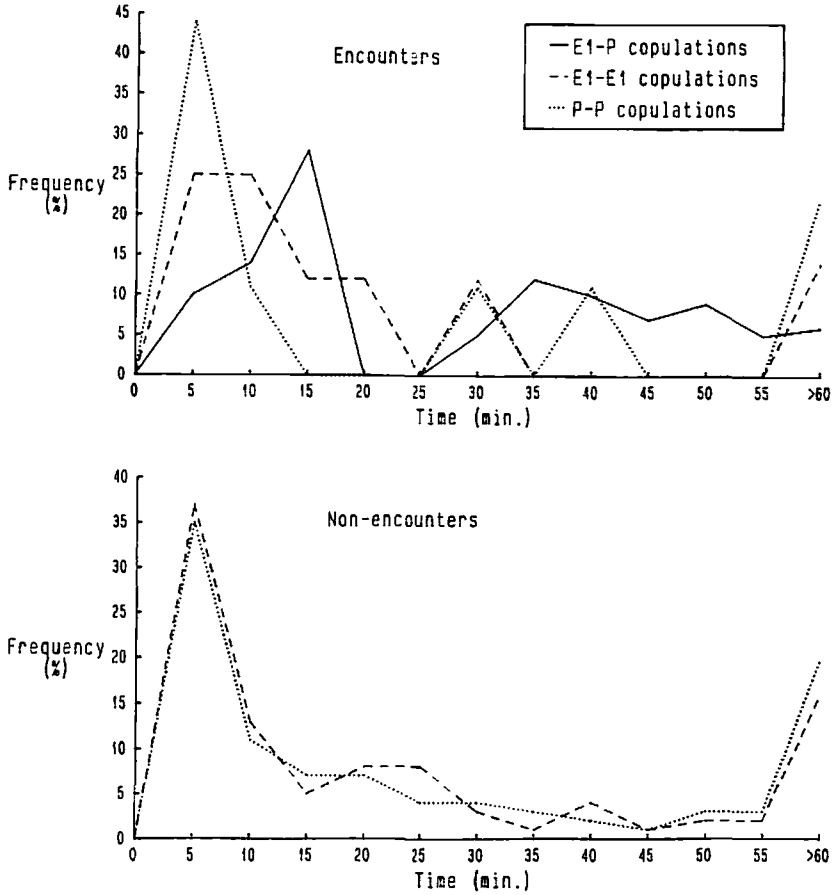

Fig. 11. Changes in inter- and intra-unit-group copulations at feeding sites. >60: Over 60 minutes. For E1–P copulations during encounters, it starts from the copulation of encounters, and for E1–E1 or P–P copulations in non-encounter contexts, it starts from the entry into the feeding sites.

together, approached *Sn*, *TN*, and *ST*, who were feeding, and also began to feed. 06:49, *TN* sat beside *Sug*, and gave her a poke in the back. *Sug* presented her rear to him. *TN* immediately copulated with her. After copulation, when *Sug* sat to resume feeding, *TN* stood upright again and displayed, inviting *Sug* to copulate. *Sug* presented again, and they copulated. After copulation, they resumed feeding there. 06:51, when *ST* approached *Sug* and peered at her. *Sug* lay on her back. *ST* mounted her and performed ventro-ventral copulation. After copulation, *ST* began feeding, while *Sug* performed GG rubbing with *Sn*.

The incidence of inter-group copulations during inter-group encounters was 43 cases (0.96 times/hr, 72%), which was much greater than the eight cases (0.18times/hr, 13 %) within E1 group and nine cases (0.2 times/hr, 15%) within P

group (Table 7; $\chi^2=59.55$, $df=2$, $p<0.01$). In both E1 and P groups, adolescent females showed the highest frequency of inter-group copulations (Fig. 12). Both groups had two adolescent females (E1, *Ki*, and *Sk*; P, *Rur*, and *Hyk*). *Ki* and *Rur*, who had recently immigrated from other groups, copulated more frequently with males of the other group than *Sk* and *Hyk*, who were still their natal groups. They also showed high frequencies of intra-group copulations (Fig. 12). *Hyk* who copulated infrequently, was still in the early stages of adolescence. *Rur* copulated more frequently than *Sug* and *No*, who showed high frequencies among parous females. The most frequent copulation partners of E1 group males were parous females of P group. Among them, *Sug* was involved in 30% of all inter-group copulations, which was statistically significant (Table 7; $\chi^2=24.34$, $df=4$, $p<0.01$). P group parous females other than *Sug* did not copulate so often. Among the parous females of E1 group, *No* copulated more frequently than other females, though the difference was not statistically significant (Table 7; $\chi^2=1.94$, $df=4$, $p>0.05$).

Three adult males of E1 group (*IB*, *MN*, and *TN*) showed significantly higher frequencies of copulation than males of other age classes (Table 7; Fig. 12; $\chi^2=32.16$, $df=2$, $p<0.01$). In the center of the feeding site, occupied by prime and old parous females, adult males of E1 group copulated more frequently than those of P group (Table 7; $\chi^2=12.16$, $df=1$, $p<0.01$). On the other hand, on the periphery, occupied by relatively young parous females, old males of P group copulated more frequently than those of E1 group (Table 7; $\chi^2=10.34$, $df=1$, $p<0.01$). Between the adolescent males of both groups, no significant inter-group difference was found (Table 7; $\chi^2=0.98$, $df=1$, $p>0.05$). In inter-individual comparison, *IB* copulated most frequently (Table 7; $\chi^2=11.44$, $df=3$, $p<0.01$). In intra-group copulations during inter-group encounters, *KLL* copulated more frequently than other males in P group (Table 7; $\chi^2=2.87$, $df=5$, $p>0.05$), while adult males copulated often in E1 group. During encounters, intra-group copulations were not observed for adolescent males in either group. In four cases, when males of P group displayed near females of E1 group, males of E1 group rushed to interrupt copulations between them; but no such cases were observed from P group males to E1 group males.

Case 6. January 14, 1987, 12:12, *TRZ* (P) approached *No* (E1), who was feeding, and displayed. When *No*, responding to the invitation, stood up to present to him, *IB* (E1) rushed to separate the two and restrained them. *No* soon left *TRZ* and went away. *TRZ* crouched to present to *IB*, but *IB* ignored him and went away.

Copulations were also observed in natural conditions between E1 and B groups in Period I, and between E1 and E2 groups in Period III. These were most frequently observed, as between E1 and E2 groups in Period II, in the excitement immediately after encounters had begun, and declined in frequency as time passed. E1 group animals who were involved in these copulations included males *KK*, *IB*, and *MN*, and females *Mt*, *Hl*, and *Bh*. Animals from the other groups could not be identified.

In Period II, five sessions of inter-group male-female grooming were observed

Table 7. Number of copulations by E1 and P group members.

E1 members	OAM				PAM			AdM			OAF			PAF						AdF	
	KK	*IK*	*KR*	*HT*	*IB*	*MN*	*TN*	*TW*	*MO*	*HO*	*Sn*	*Km*	*Mt*	*Hl*	*Sr*	*Bh*	*My*	*No*	*Ms*	*Ki*	*Sk*
Inter-group	0	0	1	0	9	1	9	0	0	5	2	1	0	1	2	0	0	3	0	5	4
Sub-total		1				19			5			3				6				9	
Intra-group	0	0	0	0	3	1	4	0	0	0	0	0	0	0	1	1	0	1	1	4	0
Sub-total		0				8			0			0				4				4	

P members	OAM			PAM					AdM			OAF					PAF					AdF	
	NPK	*HIG*	*TSB*	*SNK*	*MSP*	*TRZ*	*IDA*	*KLL*	*TNS*	*MTS*	*AJI*	*Jly*	*Hiy*	*Yub*	*Mah*	*Tsr*	*Tki*	*Sug*	*Hat*	*Moz*	*Ito*	*Rur*	*Hyk*
Inter-group	3	3	2	0	2	1	0	1	3	2	1	1	1	0	0	0	0	11	1	0	1	10	0
Sub-total		8				4				6				2					13			10	
Intra-group	1	2	1	0	1	1	0	3	0	0	0	0	0	0	0	0	0	4	1	0	0	4	0
Sub-total		4				5				0				0					5			4	

OAM: old adult male; PAM: prime adult male: AdM: adolescent male; OAF: old adult female; PAF: prime adult female; AdF: adolescent female. Sub-total means total number in each age-sex classes.

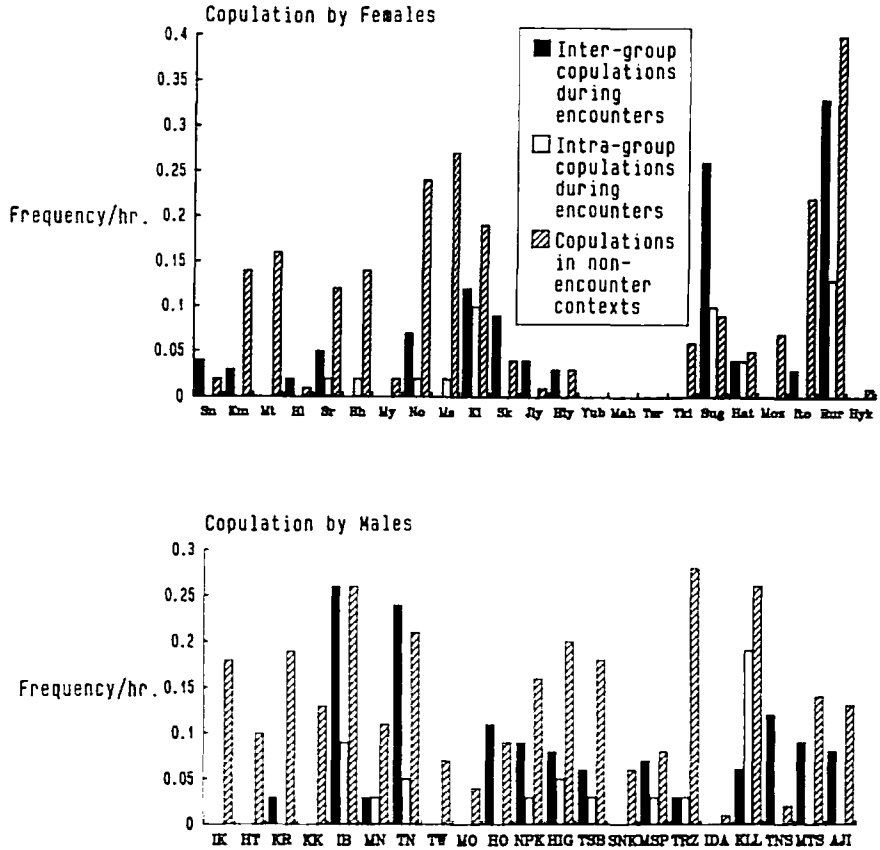

Fig. 12. Frequency of copulation by E1 and P group members. Upper: copulation by males; Lower: copulation by females.

(0.14 times/hr). The male-female pairs were *HIG-My* (30 sec.), *HIG-Mk* (47 sec.), *IB-Sug* (107 sec.), and *TN-Sug* (33 sec. and 420 sec.). In the two sessions involving HIG, the male first approached her, while, in the three involving Sug, she approached the male. The frequency of intra-group male-female grooming during encounters was 0.70 times/hr in E1 group and 0.46 times/hr in P group, which greatly exceeded that of inter-group male-female grooming sessions. However, most of the intra-group male-female grooming sessions were between mothers and their sons (65% in E1 group and 71% in P group). If these are excluded, the frequency of intra-group male-female grooming was 0.24 times/hr in E1 group and 0.14 times/hr in P group, quite similar to that of inter-group male-female grooming.

Peering behavior occurred 0.35 times/hr in inter-group contexts. In two cases a male peered at a female of the other group and they copulated, and in another a female peered at a male of the other group and they copulated. On the other hand,

in intra-group combinations, the frequency of male-female/female-male peering was 0.08 times/hr in E1 group and 0.11 times/hr in P group, much lower than that in inter-group combinations (Fig. 9). Incidentally, in both inter- and intra-group combinations, peering occurred most often between immatures or from adolescents to adults. Peering between adults accounted for only 15% of all cases.

Thirteen cases of male-female/female-male aggressive interactions were recorded (Table 6). There was a higher incidence of intra-group male-female/female-male aggression in E1 group. 41% of these cases were followed by rump-rump contact or mounting, while this was not observed in P group. In inter-group male-female or female-male aggressions, no rump-rump contact or mounting was observed. One case in which a female of P group attacked a male of E1 group was over food, and was one-to-one. Two cases in which a female of E1 group attacked a male of P group occurred when a fight between males was joined by the mother of one male. In general, in both inter- and intra-group aggression, those from males to females were mild. On the other hand, some of those from females to males were fierce, accompanied by considerable chasing, followed by beating or biting.

In addition to the above social interactions, between males and females of different groups, some cases of play, begging, and sharing of food were recorded. However, no such social interactions occurred between adult or adolescent individuals of different groups. Play was only observed between immatures, and begging was from immatures or adolescents to adults.

DISCUSSION

Various aspects of the ecology, behavior, and society of the bonobo (*Pan paniscus*) in the wild have been compared with findings for its close relative, the chimpanzee (*P. troglodytes*). Several important features have been found to be common to both species including similar group size, patrilineal social structure, and division of a unit-group to form new unit-groups (*P. t.*, Wrangham, 1979; Nishida & Hiraiwa-Hasegawa, 1987; Goodall, 1986; de Waal, 1989; *P. p.* Kuroda, 1979; Kano, 1982; Furuichi, 1987; White, 1988). On the other hand, several differences have also been found between the two species. Notable examples include the socionomic sex ratio, which is close to one in bonobos, compared with a greater number of females in chimpanzees (Nishida, 1979; Goodall, 1983), female GG rubbing behavior, which is a common behavior in bonobos, but is not seen in chimpanzees (Kano, 1980; Kuroda, 1980; Idani, in press), and infanticide and frequent meat-eating, which are characteristic of chimpanzees, but have not been observed in bonobos (Kawanaka, 1981, Takahata, 1985; Goodall, 1986; Boesch & Boesch, 1989). The present paper reveals another important difference between the two species, that found in the relations between unit-groups.

I. Friendly Relations between Groups

Relationships between unit-groups of chimpanzees are almost always an-

tagonistic (Nishida & Kawanaka, 1972; Goodall et al., 1979). In early studies of bonobos, their inter-group relationships were also thought to be antagonistic, although the extensive overlap of their home ranges, up to 60% in area, was pointed out as being quite different from chimpanzees (Kano, 1982, 1986). As research progressed, peculiar characteristics of inter-group relations gradually became apparent from fragmentary observations. Groups were observed to make auditory contact with one another, sometimes clearly avoiding a closer encounter, sometimes exchanging agonistic barks. Direct encounters were observed which led to fighting, and others that were followed by peaceful coexistence at the feeding sites. Kano (1986) stated that although their relationships may be thought to be unfriendly from the fact that grooming, copulation, GG rubbing, etc. were not observed between different unit-groups, their relationships should not be regarded as simply antagonistic because encounters did not necessarily develop into attacks, flight, or fightings.

Many instances of encounters between two unit-groups of bonobos were observed from 1986 to 1987. Most of them were observed at artificial feeding sites, and it cannot be denied that provisioning was one of the factors responsible for the encounters. However, though small in number, encounters were also observed in natural conditions. In both situations, bonobos of two unit-groups coexisted peacefully in a mixed grouping, which eventually split into the original groups. Such encounters have not been reported for chimpanzees.

In comparisons of the frequencies of GG rubbing, copulation, grooming, and peering during encounters, the incidence between groups exceeded, or differed little from that within each group. The incidence of aggressive interactions was lower between groups than within each unit-group. In bonobo society, peering, GG rubbing, and copulation are thought to function as greeting behaviors which lead to affinitive relationships by easing tension developed between individuals, or by removing uneasiness (Kuroda, 1982; Kano, 1986; Kitamura, 1989; Furuichi, 1989; Idani, in press). Grooming has been used as an index to measure affinitive relationships between females (Kano, 1980; Kuroda, 1980), as in chimpanzees. Within a unit-group, these behaviors are used to maintain peaceful relationships between kin-related and non-related individuals. Therefore, the relatively high frequency of these behaviors between individuals of different groups may allow their peaceful coexistence.

In encounters, those who took the initiative in the temporary fusion of unit-groups were females. They approached male and female individuals of the other group, and those they approached did not avoid them. Together they performed peering, GG rubbing, or copulation with males of different group, and eventually groomed each other. Through these behaviors females appeared to lower the tension developed by the encounter, leading to the formation of a fused aggregation and allowing coexistence and co-feeding. This point contrasts with the antagonistic behaviors usually shown by chimpanzee females on encounter with females of other unit-groups (Nishida & Hiraiwa-Hasegawa, 1985), although one exception has been reported (Kawanaka, 1982).

Males of different unit-groups kept a certain distance between themselves and rarely intermingled. The incidence of appeasement or reassurance behaviors such

as mounting and rump-rump contact was lower between males of different unit-groups than between males of the same group. In other words, some kind of antagonistic or unfriendly relationship apparently existed between males of the different unit-groups. However, the aggressive interactions observed between them were never as fierce as those reported for chimpanzee males of different unit-groups (Goodall et al., 1979; Goodall, 1986). Peering and rump-rump contact between males of different unit-groups, though small in number, were also recorded (Ihobe, 1990). Peaceful interactions between females appeared to ease the antagonistic mood between males of different unit-groups.

There are two more important issues to discuss. With regard to the conditions which allow temporary fusion of unit-groups in bonobos, previous reports (e.g., Kano, 1982) assumed the existence of some kind of dominant-subordinate relationship between unit-groups, as reported for chimpanzees (Nishida & Kawanaka, 1972; Goodall et al., 1979). However, in the present study, such a relationship was not observed. One group was not seen to avoid the other at the time of inter-group approaches, and two unit-groups had preferred encounters after making auditory contact. Although fighting between groups occurred after encounters, these aggressive interactions were never fierce, and did not reveal a dominant-subordinate relationship between the unit-groups. In other words, members of each group associated on equal terms during encounters. This lack of a clear dominance relationship, as well as the females' peaceful initiative, is an important factor which may enhance unit-group fusion.

The other issue is related to the sociological question of why bonobos should have such a society in which temporary fusion of unit-groups is tolerated. No special behavior patterns were observed which were unique to inter-group encounters. From the behaviors observed, this question cannot be answered. Possibly the temporary fusion of unit-groups has a sociological significance for inter-group breeding (Richard, 1976; Goodall, 1986). While chimpanzee females often move alone in the unit-group, the bonobo females aggregate with each other in the unit-group and they have a high sociability (Kano, 1980; Kuroda, 1980). Therefore, the difference in inter-group relationships between the two species may be due to the difference of inter-female relationships in the unit-group. This issue awaits further accumulation of data. Another possibility is that the temporary fusion provides young nulliparous females with opportunities for unit-group transfer.

The chimpanzee, which lives in a habitat where large food patches are rarely available, is a rather solitary forager, and this is particularly true of females (Wrangham, 1987). In contrast, the bonobo lives in a forest habitat where large food patches are available more or less continuously throughout the year. Therefore, many individuals, even of more than one unit-group, may be able to feed in one food patch at a time. Although the present paper does not present detailed ecological data, this aspect, which was apparent in encounters observed in natural settings, is undeniably a factor influencing the propensity for different unit-groups to fuse temporarily.

II. Unit-Groups

The observations presented in this paper do not imply any ambiguity in the unit-group boundary or unit-group unity in bonobos. Nor do these imply ambiguity in the unit-group identity of each individual. The data accumulated so far have revealed the firm existence of these features in the bonobo society. The data presented in this paper add the further point that they can temporarily overcome unit-group boundaries and unit-group memberships by intermingling with members of another unit-group. During the fused phase that follows, members of different unit-groups can coexist in peace. The bonobo society has sufficient flexibility to allow temporary fusion of unit-groups, and at the same time retains the unit-group structure which is resumed after the fusion.

Kuroda (1982) pointed out that the unit-group of bonobos has a dual organization. E1 group, the main study group in this study, was thought to have been a part of the E unit-group (corresponding to "subunits 1 and 2," Kano, 1982; "subgroup K," Kitamura, 1983) until 1983, and the E group was thought to have split into two (E1 and E2) independent unit-groups (Furuichi, 1987) after 1984. These two sub-units were inferred to constitute a single unit-group, because when united, they ranged together for a few days, and various social interactions were frequently performed between members of the two sub-units although the two sub-units had repeated fission and fusion. In the present study, E1 and P groups repeated fission and fusion, and various social interactions were frequently observed between them during the united phase. In other words, the relationships between "subunits 1 and 2" appears to resemble that between E1 and P groups. Moreover, no dual organization was confirmed in either E1 or E2 groups after the group division, or in P group. This raises the possibility that E group was not a unit-group comprising two sub-units, but two independent unit-groups from the beginning. However, social grooming has not been observed between males of E1 and P groups, while grooming was observed between the males of sub-units 1 and 2. This could turn out to be an important difference between groups and sub-units of bonobos, and should be examined in future investigations.

Considering the evolution of human society, Imanishi (1961) listed four criteria which distinguish it from other forms of animal society. One of them was the existence of community, a kind of regional society linking several social units through neighborhood relationships. (Note that this usage of "community" differs from that of some chimpanzee researchers [e.g., Goodall, 1986] who have used it synonymously with "unit-group" [Itani, 1980]). Although gelada baboons (Crook, 1966; Kawai et al., 1983) and hamadryas baboons (Kummer, 1968), have "herds" or "troops," which show harmonious neighborhood relationships (such as foraging of several unit-groups together), they retain unit-group boundaries, showing no inter-unit-group fusion (Itani, 1982). In societies of African great apes other than bonobos, only antagonistic relationships have been reported between unit-groups (Nishida & Kawanaka, 1972; Goodall et al., 1979; Fossey, 1979; Yamagiwa, 1987). Although the structure of the assumed "community" above the unit-group level in bonobos has not been fully revealed, their neighborhood relationships which allow peaceful coexistence of two unit-groups provide the first

nonhuman primate community model which is close to Imanishi's (1961) model of human society.

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